ON THE PHYLOGENETIC AFFINITY OF THE EXTINCT ACRODONTAN LIZARD *TINOSAURUS*

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ABSTRACT

North American species of the fossil lizard taxon *Tinosaurus* have been considered as indeterminate agamids or acrodontans for nearly a century. New material from the late Eocene Chadron Formation of North Dakota, USA, may provide the first glimpse of non-dental cranial elements of this taxon and so new information on the affinity of North American *Tinosaurus*. The ectopterygoid is most securely referred and shows a unique apomorphy of extant *Leiolepis* (butterfly lizards): a dual articulation of the pterygoid on the ectopterygoid. Other elements show a mosaic of sometimes conflicting apomorphies. Ultimately, the evidence provided by the new elements on the phylogenetic position of North American *Tinosaurus* is not strong, and some of them might pertain to a co-occurring iguanid lizard, *Cypressaurus* sp. MPH. Even if further work were to turn up more support for a union of *Leiolepis* and North American *Tinosaurus*, this would not necessarily apply to any nominal species of *Tinosaurus* outside of that continent. If *Tinosaurus* actually is related to *Leiolepis*, it constitutes another example of a modern tropical taxon with extratropical stem representatives in the greenhouse world of the Eocene.

Key words: Squamata, Iguania, Agamidae, Tinosaurus, *Eocene, dispersal, climate change, North America, Asia.*

INTRODUCTION

Acrodonta, comprising the possibly paraphyletic taxon Agamidae* (agamas, dragons, mastigures, etc.) and Chamaeleonidae, is today an exclusively Old World clade of lizards (e.g., Moody 1980). Leidy (1872), however, recognized that a species represented by a jaw fragment from the Eocene Bridger Formation of Wyoming, USA, is also referable to the group. He erected the name *Chamaeleo pristinus* for it and later (1873) gave the specimen a fuller description. He did not realize, however, that Marsh (1872) had previously named (but not figured) a new "carnivorous lizard," *Tinosaurus stenodon*, also from the Bridger, which likely pertained to the same lineage. Estes (1983) questioned the distinction of the two species but did not formally synonymize the former with the latter. Camp (1923) concluded that *Tinosaurus* could not be distinguished from either *Chamaeleo* (Chamaeleonidae) or *Calotes* (Agamidae*), implicitly questioning the diagnostic value of the type material. *Tinosaurus* has subsequently been recognized throughout the Eocene of North America (Gunnell & Bartels 1999; Gunnell & Bartels 2001; Hirsch *et al.* 1987; Kelly *et al.* 1991; McGrew *et al.* 1959; Moody 1980; Pearson 1998; Schatzinger 1975; Smith 2006a, b), although no new species have formally been named. On the other hand, a host of new nominal species has been referred to the genus from the Old World (Augé & Smith 1997; Averianov 2001; Dong 1965; Hou 1974; Li 1991; Li & Xue 2002; Prasad & Bajpai 2008), primarily on the basis of tricuspid, acrodont cheek teeth and early Tertiary age (Estes, 1983).

The chief difficulty in understanding "*Tinosaurus*" is that tricuspid teeth of a similar form are probably present in some 200 living species of Agamidae*, principally those species placed in Draconinae and *Leiolepis* (Smith *et al.* 2011), following the taxonomy of Macey *et al.* (2000). No other features of phylogenetic significance are known, which partly relates to the fact that the only described elements of *Tinosaurus* are from the jaws. At the present time, even polyphyly of "*Tinosaurus*" cannot be excluded. Although it is necessarily true that species of "*Tinosaurus*" have definite affinities with extant clades, no data are available that would link any nominal species of the genus to a particular clade.

In this paper I refer non-dental cranial remains of a species of *Tinosaurus*, in particular one from North America, for the first time. The material was discovered during recent examination of bone concentrate derived from screenwashing of the late Eocene Chadron Formation of North Dakota by crews of the Pioneer Trails Regional Museum under the direction of Dean Pearson. The material pertains to the Medicine Pole Hills local fauna, which was already known to preserve remains of a species of *Tinosaurus* (Pearson 1998; Smith 2006b). After describing the material, I present detailed comparative osteological observations on living acrodontan lizards (Appendix), and analyze the implications of the new character data for the relationships of North American *Tinosaurus* and their potential significance for biogeography and divergence times in Acrodonta.

For modern comparative specimens examined, see Appendix. Institutional abbreviations: CM: Carnegie Museum of Natural History – Herpetology, Pittsburgh, Pennsylvania, USA; PTRM: Pioneer Trails Regional Museum, Bowman, North Dakota, USA; SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany; UF: University of Florida Museum of Natural History, Gainesville, Florida, USA.

SYSTEMATIC SECTION

Squamata Oppel 1811

Iguania Cope 1864

Agamidae Spix 1825

Genus *Tinosaurus* Marsh 1872

Tinosaurus sp. MPH
[after Pearson 1998, Smith 2006a]

Figs. 1, 3, 5, 7

Newly referred specimens. PTRM 19083 (jaw fragment), 19112 (partial frontal; Fig. 7d), 19113 (partial frontal; Fig. 7a–c), 19134 (partial right ectopterygoid; Fig. 5), 19203–19205 (jaw fragments), 19307 (partial premaxilla), 19340 (left maxilla fragment; Fig. 3), 19429 (partial premaxilla), 19467 (frontal fragment), 19515 (partial premaxilla; Fig. 1), 19533 (right maxilla fragment).

Comments. These specimens, like all those recovered by screenwashing, are isolated from one another and fragmentary. Smith (2009a) briefly reviews the reasons for the secondary association of such isolated vertebrate remains. In the case of the Medicine Pole Hills local fauna, the chief difficulty in associating the remains at hand is the existence of a second, not uncommon iguanian species in the locality, *Cypressaurus* sp. MPH (Smith 2011), to which they could also plausibly be attributed. In fact, the number of identified dentigerous elements of *Cypressaurus* sp. MPH markedly exceeds that of *Tinosaurus* sp. MPH; relative abundance, then, might even favor the former species. Many acrodontan isolated elements are scarcely distinguishable from their counterparts in Iguanidae. However, in each case there appear to be subtle features inconsistent with typical morphologies in Iguanidae but concordant with Acrodonta or some part thereof. Thus, I provisionally refer them to that taxon, recognizing that the study of more numerous or complete elements from this locality or specimens of *Tinosaurus* from other North American localities could necessitate a revision in which some of these elements are referred to *Cypressaurus* sp. MPH.

In the following, I have assumed that only a single species of acrodontan was present in the locality. It is true that many modern localities feature more than a single species of acrodontan. However, there is no evidence that North America was colonized by more than one species, and no evidence that the lineage it spawned (*Tinosaurus*) was ever represented by more than a single species in a locality. The size of the specimens does not contradict their pertaining to a single species, nor are distinct morphotypes apparent where more than one specimen of an element is known. The most parsimonious interpretation is that all acrodontan specimens represent a single species. It is referred to *Tinosaurus* under the assumption that only a single lineage of Acrodonta ever reached North America (see Smith 2006a), which is parsimonious but not clearly demonstrable at present. Informal nomenclature follows Smith (2006a), with "MPH" referring to the Medicine Pole Hills. Smith (2009a) notes that the common practice of writing "*Genus* sp." is informal and not governed by the ICZN. The "MPH" provides a convenient short-hand for specifying a population even if it is not well enough preserved to warrant a formal name.

Description of new elements. *Premaxilla.* Three premaxillae are associated here. They are considered to represent an iguanian because of the morphology, which compares well to Iguania but is inconsistent with the anguid *Peltosaurus*, the only other taxon known from the locality that is large enough and present in sufficient abundance to have produced this premaxillary morphotype. The apomorphic presence of a posterior shelf with dorsal facet (see below) supports referral to Acrodonta rather than to Iguanidae. Most of the description, except where otherwise indicated, comes from the more complete PTRM 19515.

Description: The smallest specimen (PTRM 19429) is 2.2 mm across the main body, the largest (PTRM 19515) 4.4 mm. The anterior margin of the bone is distinctly curved in dorsal view (Fig. 1a). It extends nearly dorsally from just above its ventral edge (it is only weakly convex in sagittal cross-section), then curves abruptly toward the posterior (Fig. 1b). The nasal process (n.pr.), only the base of which is preserved, extends posterodorsally; its anterior surface is weakly convex in cross-section (Fig. 1b, c). A facet for the nasal is not present on the preserved portion of the nasal process (Fig. 1d). Lateral to the base of the nasal process on each side is a pair of tiny foramina, which presumably correspond to the posterior premaxillary foramina (p.pm.f.) of Bahl (1937); through them the maxillary artery and a portion of the ethmoidal nerve entered. On the left side of PTRM 19307 that foramen is single, not double. Lateral to these foramina is a rounded ridge that extends to the lateral-most margin of the bone and

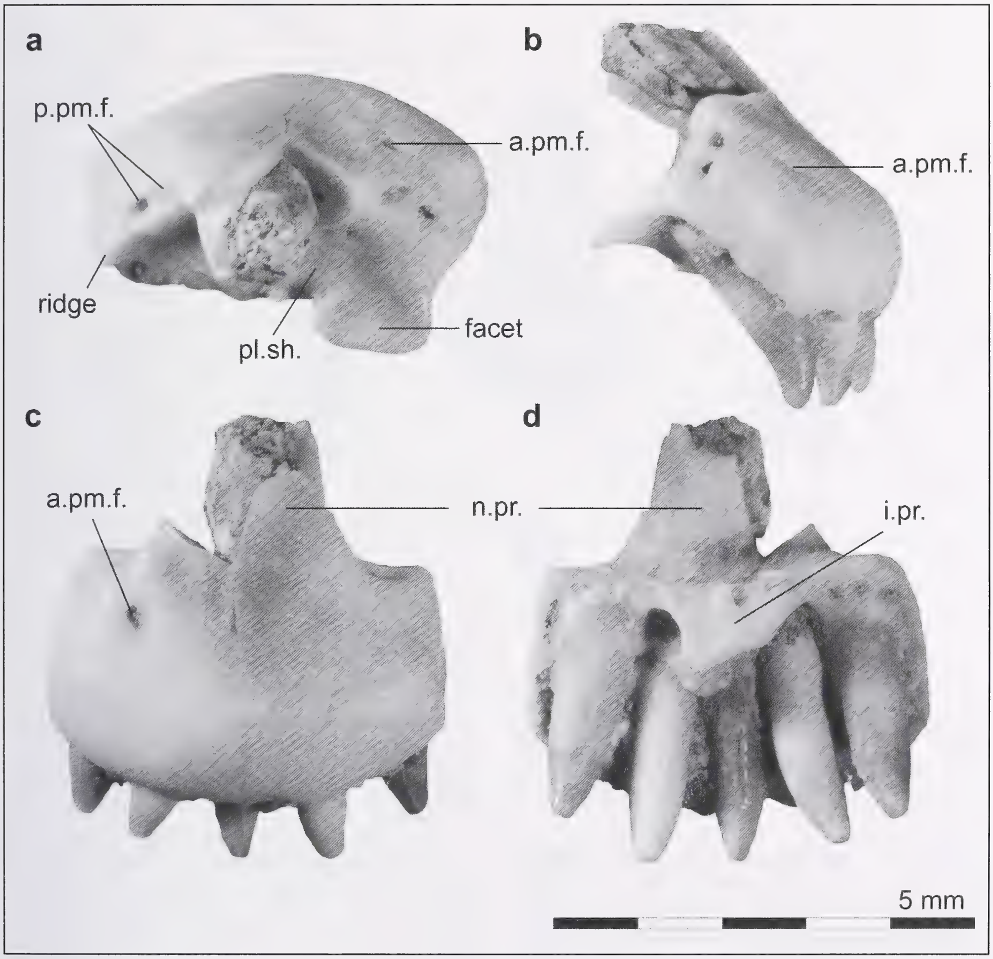

FIG. 1. Partial premaxilla of *Tinosaurus* sp. MPH, PTRM 19515, in (a) dorsal, (b) right lateral, (c) anterodorsal, and (d) posteroventral views. Abbreviations: a.pm.f., anterior premaxillary foramen; i.pr., incisive process; n.pr., nasal process; pl.sh., palatal shelf; p.pm.f., posterior premaxillary foramen.

divides the maxillary articulation into a large labial portion and a small lingual one (Fig. 1a). The maxillary articulation does not appear to run up the lateral edge of the nasal process, which is somewhat surprising. All acrodontans have a strong dorsal projection at the anterior end of the premaxillary process of the maxilla which articulates on the lateral surface of the premaxilla (Evans *et al.* 2002). However, in most taxa the ethmoidal nerve exits the nasal capsule onto the snout through a dorsoventrally elongate foramen located between the premaxilla and the dorsal projection of the maxilla. Thus, the articulation between premaxilla and maxilla along the projection is not continuous (except in *Uromastyx*[1], in which the ethmoidal nerve penetrates the premaxilla and forms a pair of foramina on its anterior surface, and *Physignathus cocincinus* and perhaps a few other taxa, where the foramina appear to be greatly reduced or absent). The absence of a dorsal maxillary articulation in *Tinosaurus* sp. MPH suggests that these foramina were located low on the snout. On the right side of PTRM 19515 only there is a small anterior premaxillary foramen (a.pm.f.), which would have transmitted a branch of the ethmoidal nerve onto the snout.

Posterior to the nasal process is a shelf, weakly dorsally concave in transverse section (Fig. 1a, pl.sh.). Along the anterior margin of this shelf, at the base of the nasal process, is a curvilinear series of about five tiny foramina. Posteriorly the shelf is divided by a wide median cleft. On either side of the cleft is a posterior continuation of the palatal shelf whose dorsal surface is marked by a weak oval depression (facet) for articulation with the maxilla. A pair of struts projects ventromedially from the underside of the posterior continuation of the shelf (Fig. 1d). These struts fused on the midline to form a distinct, anteroposteriorly compressed, tabular incisive process (i.pr.). On the dorsal edge of this plate is a peg-like projection that extends as far dorsally as the dorsal surface of the palatal shelf. Anterior to this projection is a foramen that runs dorsoventrally through the palatal shelf.

Both of the more complete specimens had five simple, pleurodont teeth (Fig. 1c, d). These teeth are stocky. Their bases are circular in cross-section. Just below the jaw parapet they begin to taper, terminating in conical tips; the tips are distinctly posteriorly decurved, sometimes also with a distal component (e.g., first right tooth: Fig. 1d) which gives them a diverging appearance. No carinae or striae are evident. The base of the first right tooth appears to be eroded, indicating that tooth replacement was in progress.

Comparisons: The size of the lateral processes of the premaxilla varies significantly in Acrodonta (Siebenrock 1895). In *Leiolepis* these are relatively stronger (Fig. 2b, l.pr.) than many other acrodontans, including Agaminae (Fig. 2a) and *Uromastyx* (Fig. 2c). Consequently, it also possesses a greater number of teeth: four teeth are present in each available specimen of *L. belliana,* whereas most other examined acrodontans have no more than three (except *Japalura polygonatus*, also with five, and some *Uromastyx*). Siebenrock (1895) lists only a few other taxa with four or more premaxillary teeth: *Hydrosaurus,* several members of Amphibolurinae (one species each of *Ctenophorus, Amphibolurus, Pogona*), and one species of *Gonocephalus. Tinosaurus* sp. MPH is thus similar to *Leiolepis* and a few other living acrodontans in having >3 teeth. Outgroup comparisons with Iguanidae (Smith 2009b) and stem acrodontans from the Late Cretaceous of Mongolia (Alifanov 1989; Borsuk-Białynicka & Moody 1984; Gao & Norell 2000) suggest that the condition of having large lateral processes and a high tooth count is plesiomorphic. However, its interpretation in *Leiolepis* depends in part on the phylogenetic position of that taxon.

Uromastyx appears to be distinctive in Acrodonta in commonly having anterior premaxillary foramina (Fig. 2f). I may have erred in stating that these are also present in *Leiolepis* (Smith, 2009a), for they are absent in the three specimens currently available to me (Fig. 2e). They only occasionally occur in other agamids, such as unilaterally in one *Trapelus pallidus* (CM 41289). The unilateral presence of a foramen in one of three specimens of *Tinosaurus* sp. MPH provides some evidence that this taxon is related to *Uromastyx*, but under a frequency-coding scheme (e.g., Poe 2004) this support would be considerably less than one full step. Furthermore, the single foramen found in PTRM 19515 is relatively small in comparison with those seen in *Uromastyx* and most iguanids with such foramina.

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[1] Wilms *et al.* (2009) recently revised the generic taxonomy of *Uromastyx*, placing three species, *U. hardwickii, U. asmussi,* and *U. loricata,* which had been considered basal in the genus (Moody 1980, 1987) and which Wilms *et al.* determined to form a clade, in the genus *Saara* Gray (type species: *Saara hardwickii*). For the present I follow the TIGR Reptile Database (Uetz *et al.* 2007) in retaining those species in *Uromastyx.*

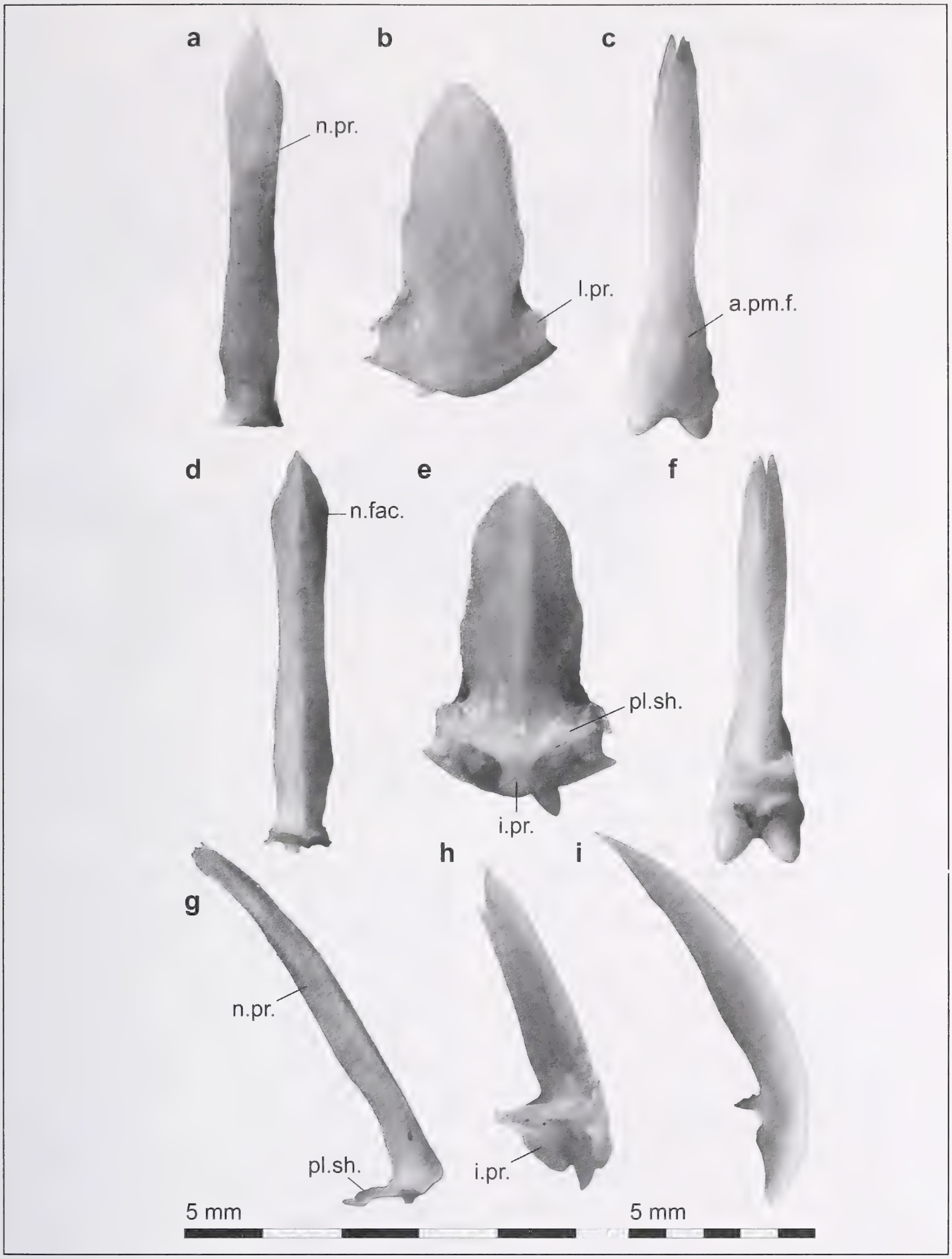

FIG. 2. Premaxillae of select agamids in anterodorsal (upper row), posteroventral (middle row), and right lateral (bottom row) views. (a, d, g) *Agama mossambica*, UF 55339; (b, e, h) *Leiolepis belliana*, UF 62048; and (c, f, i) *Uromastyx princeps*, CM 145044. Abbreviations: a.pm.f., anterior premaxillary foramen; i.pr., incisive process; l.pr., lateral process; n.fac., nasal facet; n.pr., nasal process; pl.sh., palatal shelf; p.pm.f., posterior premaxillary foramen.

The occurrence of a distinct incisive process is quite variable in agamids. One is present in many Agaminae (e.g., *Laudakia stellio, Pseudotrapelus sinaitus*) but highly reduced to absent in others (e.g., *Agama mossambica*: Fig. 2d); present in most (all?) Draconinae; present in *Leiolepis* (Fig. 2e) but absent in *Uromastyx* (Fig. 2f); present in *Hydrosaurus amboinensis*; and present but rather small in *Physignathus cocincinus* and *Pogona vitticeps* (Amphibolurinae). An incisive process is absent in Chamaeleonidae. The presence of an incisive process and its flattened shape in *Tinosaurus* sp. MPH offer little guidance at this point.

The medial apposition of the maxillae behind the premaxilla, recognized early by Siebenrock (1895) as a characteristic of Agamidae*, is also found in Chamaeleonidae (Frost & Etheridge 1989; Siebenrock 1893). (Contact appears to have been lost in a few taxa: see Bell *et al.* 2009.) In these taxa the anteromedial processes of the maxilla are expanded; they partly rest dorsally on the palatal shelf of the premaxilla but also extend posteriorly beyond it. In *Uromastyx* and *Leiolepis*, additionally, the palatal shelf is cloven between the facets for the maxilla, a characteristic that does not occur in examined draconines, amphibolurines (*Pogona vitticeps* and *Physignathus cocincinus*), *Hydrosaurus amboinensis*, or most agamines (except *Laudakia stellio*). However, the feature cannot be evaluated in Chamaeleonidae because the palatal extent of the premaxilla is so highly reduced. The occurrence of cleavage in *Tinosaurus* sp. MPH suggests possible affinity with *Leiolepis* and *Uromastyx*, but additional outgroup comparison is desirable. The exact form of the rounded facets for the maxilla distinguishes *Tinosaurus* sp. MPH from both *Leiolepis* and *Uromastyx*, where the facets are deep, longitudinal indentations immediately adjacent to the median cleft, close to the condition seen in other agamids. No other acrodontan available as a disarticulated skeleton showed facets of a similar form, and they may be an autapomorphy of *Tinosaurus* or some part of it.

The position of the posterior premaxillary foramina in *Tinosaurus* sp. MPH appears somewhat unusual for Iguania, where, as in most other lizards, they are generally located more medially, hidden behind the nasal process. It is possible that a laterally displaced position of these foramina is related to the transformation of the anterior end of the maxilla. It is observed, for instance, that the dorsal process at this end of the maxilla is frequently bifurcated (Smith 2009b), presumably for the subnarial artery. The foramina appear to be laterally displaced in *Leiolepis* (Fig. 2e). Yet, at least some agamids (e.g., *Bronchocela cristatella*) have more normally disposed foramina, and insufficient disarticulated specimens were available to determine if the *Tinosaurus* condition is the rule in Acrodonta.

The posterior and distal decurvature of the tooth tips that causes an appearance of divergence is not uncommon among agamids and was found in *Physignathus cocincinus* and *Leiolepis belliana* (Fig. 2e), among taxa with at least three premaxillary teeth.

Maxilla. Two specimens can be identified as maxillae (Fig. 3). (Other dentigerous specimens are too fragmentary.) The more complete of them, PTRM 19340, is a posterior fragment of a left element that, based on adhering sediment, was probably broken prior to burial. The anterior break passes through the posterior end of the palatine process. The description, unless otherwise noted, is based on this specimen.

Description: The dorsal margin of the posterior remnant of the facial process trends straight posteroventrally (Fig. 3a, b, f.pr.). Just above the level of the palatal shelf (Fig. 3b, c, pl.sh.) there is a sudden inflection (infl.) toward the ventral, and where the dorsal margin drops below the level of the palatal shelf, it begins to curve posteriorly. The inflection point probably marks the boundary between the lacrimal and jugal, although such an inflection is also seen in agamids that appear to lack an ossified lacrimal (e.g., *Pogona vitticeps*). The facial process thus lacks a reentrant on the jugal (see Smith 2009b). The jugal groove (Fig. 3b, j.gr.) is deep posteriorly, extending well below the horizontal level of the anterior portion of the palatal shelf; it is also exposed laterally (Fig. 3a), because the facial process is completely decayed posteriorly. The jugal groove shallows anteriorly and rises along with the palatal shelf, which is more dorsally located anteriorly than posteriorly. The medial edge of the shelf is broadly rounded anteriorly but becomes dorsoventrally compressed posteriorly (Fig. 3c). The shelf curves sharply medially at the anterior-most preserved end of the bone, forming part of the palatine process (Fig. 3b, pl.pr.), but there is no evidence of a facet for the palatine articulation. PTRM 19533, which preserves a slightly more anterior portion of the bone than PTRM 19340, evinces a small superior alveolar foramen (SAF), presumably the posterior-most of many, near the anterior end of the palatine process, which is

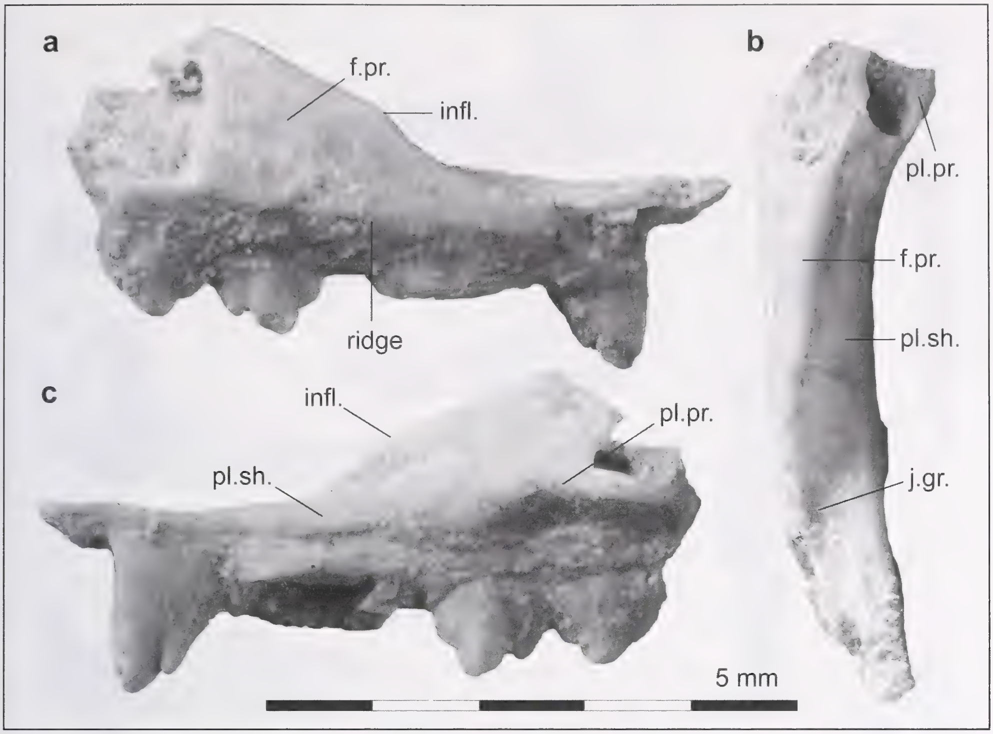

FIG. 3. Left maxilla fragment of *Tinosaurus* sp. MPH, PTRM 19340, in (a) lateral, (b) dorsal, and (c) medial views. Abbreviations: f.pr., facial process (posterior remnant); infl., inflection point; j.gr., jugal groove; pl.sh., palatal shelf; pl.pr., palatine process.

roughly twice as long as a tooth in the same portion of the bone; the same specimen also preserves what is probably the last labial (alveolar) foramen at the same transverse level as the ultimate SAF. The lateral face of the bone is divided into two surfaces by a longitudinal ridge (Fig. 3a); dorsal to the ridge is the laterally directed facial process, ventral to it is a ventrolaterally directed surface. In PTRM 19533 the distance between the jaw parapet and this ridge decreases anteriorly.

Tooth morphology is similar to that previously described for this taxon (Pearson 1998). Tooth implantation is pleuracrodont. The teeth increase in mesiodistal length as well as apicobasal height posteriorly. The lingual tooth surfaces are not well preserved, which probably reflects both wear in life as well as postmortem damage.

Comparisons: PTRM 19340 differs from the maxilla of most agamids in that the palatine facet does not appear to extend to the posterior end of the palatine process of the maxilla. In examined Agaminae (Fig. 4a), *Hydrosaurus*, Amphibolurinae, Draconinae and *Uromastyx* (Fig. 4c), the maxillary process of the palatine is medially extensive posteriorly, so that the facet it forms is found along the entire posterior margin of the palatine process of the maxilla. In contrast, the facet does not extend to the posterior margin of the process in *Leiolepis* (Fig. 4b). This is additionally the case in Chamaeleonidae. Unfortunately, the palatine process is incomplete in both fossil specimens, so this observation must be regarded as tentative.

The posterior remnant of the facial process of the maxilla in Agaminae (Fig. 4d), *Hydrosaurus*, Amphibolurinae, Draconinae and *Uromastyx* (Fig. 4f) bears a reentrant on the jugal, but this is lacking in *Leiolepis* (Fig. 4e; Smith 2009b). The reentrant is lacking in *Tinosaurus* sp. MPH, in Chamaeleonidae, and rarely in other agamids (e.g., *Moloch horridus*;

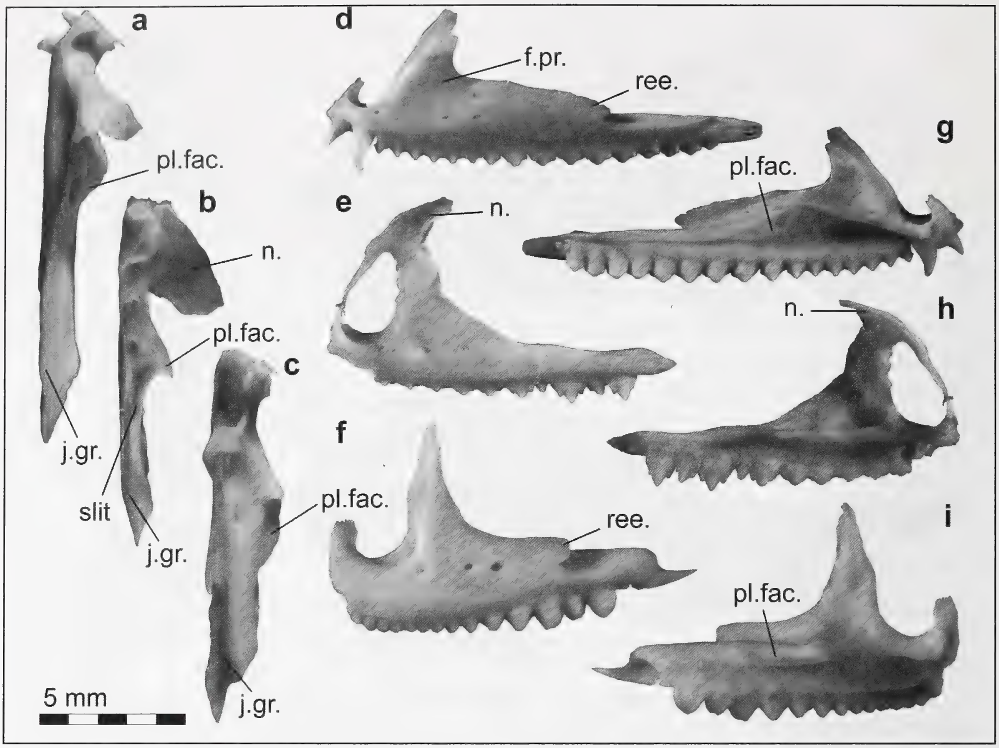

FIG. 4. Maxillae of select agamids in dorsal (left column), lateral (middle column), and medial (right column) views. (a, d, g) *Agama mossambica*, UF 55339; (b, e, h) *Leiolepis belliana*, UF 62048; and (c, f, i) *Uromastyx princeps*, CM 145044. Abbreviations: f.pr., facial process (posterior remnant); j.gr., jugal groove; pl.pr., palatine process; ree, maxillary reentrant on the jugal.

Bell *et al.* 2009). It is unclear whether this feature is autapomorphic of Agamidae* and lost in *Leiolepis*, or whether the state in *Leiolepis* is plesiomorphic. Among living agamids, however, *Tinosaurus* sp. MPH is uniquely similar to *Leiolepis* in this respect.

The posterior remnant of the facial process extends posteriorly well beyond the palatine process in most agamids (although posterior to the reentrant it is completely absent). In *Leiolepis*, however, the posterior extent of the facial process is reduced, extending no farther than the posterior end of the palatine process, fully exposing the jugal in lateral view. The length of the facial process in *Tinosaurus* sp. MPH is intermediate in length, which incidentally shows that there is no simple relationship between facial process length and the presence of a reentrant.

In at least some specimens of *Leiolepis*, there is a longitudinal slit on the dorsal surface of the (narrow) palatal shelf (Fig. 4b). This slit is located midway between the palatine process and the posterior end of the bone. Re-articulation of UF 62048 reveals that the slit receives neither the edge of the jugal nor the ectopterygoid; its presence is presumably related to a yet undetermined feature of the connective tissue. This slit was not found in other agamids available as disarticulated specimens and is absent in *Tinosaurus* sp. MPH. This absence is considered plesiomorphic.

Ectopterygoid. A single, partial right ectopterygoid, PTRM 19134, is associated with this species on the basis of size and its consistency with morphologies commonly encountered in Agamidae* (see below). The bone is lacking parts of the anterolateral and posterolateral processes as well as much of the pterygoid process (Fig. 5).

Description: The maxillary facet (Fig. 5a, mx.fac.) is broad on the ventral surface of the lateral process. Its medial margin is convex, its lateral one straight to weakly concave. The facet is at a high angle to the horizontal (Fig. 5b). A weak lip is developed where the maxillary facet terminates in line with the main body of the bone (Fig. 5a). The lip grows in prominence posteriorly, but the ventral corner of the posterolateral process (Fig. 5a, c, pl.pr.) is then truncated by breakage. The extent of the ventral corner of the process cannot be determined, but it appears to have been more massive than the dorsal corner. The lateral surface of the bone, which articulated with the medial surface of the jugal, is oblique, directed laterally and slightly dorsally (Fig. 5d, j.fac.). Near its posterior end the jugal facet is concave, but moving onto the anterolateral process it is flat, except for a shallow groove just below the dorsal margin. The posterior concave portion is traversed by a small groove that arches from anteroventral to anterior and gives off a few minor branches. The ventrolateral edge of the bone is drawn out into a thin flange, the maxillary and jugal facets meeting one another at an acute angle (Fig. 5b).

The main body of the bone has a slightly convex anterior margin and a concave posterior one (Fig. 5a). The posterior concavity forms the coronoid recess (cn.rec.), which receives the coronoid bone and associated tissues when the jaw is adducted. The surface of the recess is nearly vertical medially but becomes oblique (anteroventral) laterally. At the medial end of the main body are two facets for articulation with the pterygoid, each with a tapering, rounded lateral terminus. The one on the posterior side of the bone is the primitive pterygoid facet (Fig. 5a, c, pt.fac.p.). The one on the anterior side extends just as far laterally as the first (pt.fac.a.). These distinct portions of the pterygoid articulation are separated by a transverse flange of bone whose medial edge is not preserved, and indicate that the pterygoid possessed an additional articular projection in the space between the lateral process of the bone and its anterior part.

The dorsal surface of the bone is flat and smooth (Fig. 5c).

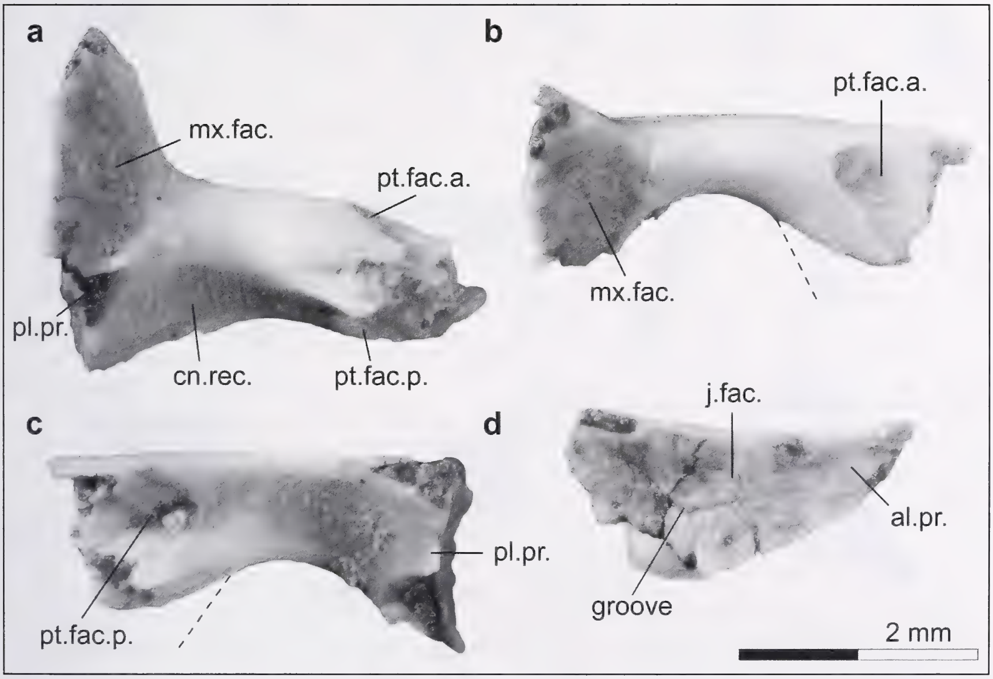

FIG. 5. Partial right ectopterygoid of *Tinosaurus* sp. MPH, PTRM 19134, in (a) ventral, (b) anterior, (c) posterior, and (d) lateral views. Abbreviations: al.pr., anterolateral process; cn.rec., coronoid recess; j.fac., jugal facet; mx.fac., maxillary facet; pl.pr., posterolateral process; pt.fac.a., anterior portion of pterygoid facet; pt.fac.p., posterior portion of pterygoid facet.

Comparisons: By retaining a posterolateral process, this ectopterygoid is plesiomorphic in comparison with Scleroglossa (Smith 2006b), the sister-taxon to Iguania. Although plesiomorphy cannot be used to unite two taxa, I consider it unlikely that PTRM 19134 represents a long-surviving previously unknown lineage of stem-acrodontan or some other lepidosauromorph other than Iguania. Subtle features of this ectopterygoid, in turn, suggest its referral to Acrodonta rather than Iguanidae within Iguania. In iguanids the medial margin of the anterolateral process of the bone usually curves fairly continuously medially to form the anterior margin of the bone, whereas in agamids the change in orientation tends to be more abrupt (Fig. 6a, b). That is to say, the anterior margin of the bone and the medial margin of the anterolateral process can usually be described by a single radius of curvature in iguanids, but in agamids they cannot. This generality holds fairly well, although the agamid condition is not quite so clear

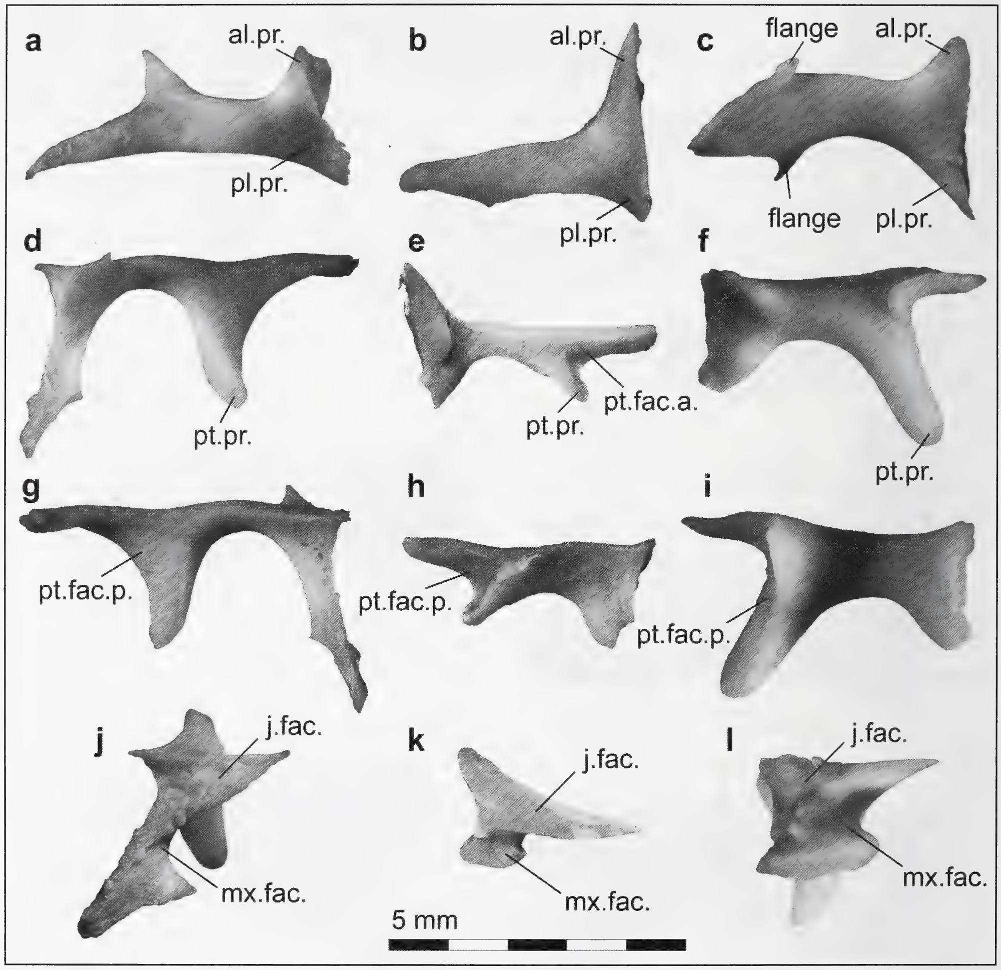

FIG. 6. Ectopterygoids of select agamids in dorsal (first or upper row), anterior (second row), posterior (third row), and lateral (fourth or bottom row) views. (a, d, g, j) *Agama mossambica*, UF 55339; (b, e, h, k) *Leiolepis belliana*, UF 62048; and (c, f, i, l) *Uromastyx princeps*, CM 145044. Abbreviations: al.pr., anterolateral process; cn.rec., coronoid recess; j.fac., jugal facet; mx.fac., maxillary facet; pl.pr., posterolateral process; pt.fac.a., anterior portion of pterygoid facet; pt.fac.p., posterior portion of pterygoid facet; pt.pr., pterygoid process.

in *Uromastyx* (Fig. 6c), and the iguanid condition is not always found in that clade. PTRM 19134 conforms to the agamid condition. Furthermore in Acrodonta, the anterior margin of the neck of the bone and the medial margin of the anterolateral process tend toward a right angle (like in PTRM 19134), where as the angle is usually obtuse in Iguanidae. Another agamid characteristic of PTRM 19134 is the extreme thinness of the ventrolateral edge of the bone (also absent in *Uromastyx*). Finally, the slightly dorsally arched character of PTRM 19134 (Fig. 5b) is fully consistent with Acrodonta but totally inconsistent with Iguanidae. These are the primary reasons for associating PTRM 19134 with Acrodonta, and hence *Tinosaurus* sp. MPH.

The additional articular projection of the pterygoid on the ectopterygoid, as indicated by the dual articulation facet in PTRM 19134, is also found in *Leiolepis belliana* (Fig. 6e). A dual articulation is not directly observable in articulated specimens (UF 62046, 62047, SMF 57471), but even here the semitranslucency of the bone allows determination of where the pterygoid terminates medially and so provides a strong indication of this reinforced relationship between the two elements. In UF 62048 (the only available disarticulated specimen of *L. belliana*), the two portions of the facet have an approximately equal lateral extent and are separated by a sharp, transverse ridge (Fig. 6e, h). An anterior articulation of the pterygoid on the ectopterygoid appeared to be absent in all examined members of Agaminae (Fig. 6d), Draconinae, Amphibolurinae, and *Hydrosaurus*. As far as I am aware, this dual articulation otherwise only occurs in *Dipsosaurus dorsalis* and part of its stem, including the stem taxon *Queironius praelapsus*, also known from the Medicine Pole Hills local fauna (Smith 2011).

Differently derived is the condition in *Uromastyx*, where the pterygoid articulation on the ectopterygoid is also visible anteriorly. In most examined species of the latter taxon, however, the pterygoid articulates entirely on a curious flange found on the anterior margin of the ectopterygoid (Fig. 6c). The primitive posterior articulation of the pterygoid also is braced by a strong, posteriorly directed flange on the ectopterygoid (Fig. 6c). As far as I am aware, these ectopterygoid flanges are unique to *Uromastyx* in Iguania, although a smaller projection in *Moloch horridus* (Bell *et al.* 2009) may be analogous to the anterior flange in *Uromastyx*. In *U. acanthinura, U. princeps*, and most probably *U. geyri*, the anterior and posterior facets for the pterygoid are confluent, i.e., they are not separated by a sharp transverse ridge; in *U. hardwickii*, on the other hand, a broad, rounded ridge is in fact developed between them. In summary, the condition seen in *Tinosaurus* sp. MPH appears to be found only in *Leiolepis* among living acrodontans, but the equally unique condition in *Uromastyx* could have been derived from it, especially considering the basal (Amer & Kumazawa 2005b; Moody 1987) position of *U. hardwickii.*

Usually in Agamidae* (Fig. 6j, l), but not Chamaeleonidae, the ventral corner of the posterolateral process of the ectopterygoid is greatly enlarged (and varies considerably in morphology). In *Leiolepis*, in contrast, the ventral corner (particularly when the flange bearing the maxillary facet is excluded) is relatively smaller. Although both dorsal and ventral corners of this process are broken in PTRM 19134, it appears that the ventral one may have been the stronger (see above), as in most agamids. This is presumably a primitive feature of *Tinosaurus* sp. MPH. The morphology of the ventral corner holds more information, which will become useful when this portion of the bone becomes known in *Tinosaurus*.

Tinosaurus sp. MPH, like *Leiolepis* (Fig. 6h) and *Uromastyx* (Fig. 6i), lacks the extreme dorsoventral thinness and rounded ventral edge of the central portion (neck) of the ectopterygoid which is seen in many Agaminae (Fig. 6g), Draconinae, and Amphibolurinae. In this respect, *Tinosaurus* sp. MPH is also presumably primitive.

The maxillary facet on the ventral surface of the lateral portion of the ectopterygoid faces roughly ventrally in most agamids available as disarticulated skeletons (Fig. 6d). (The condition in chameleons is difficult to evaluate, because the maxillary facet is so highly reduced.) In *Leiolepis*, the medial portion of the maxillary facet also faces ventrally, but laterally the facet curves strongly ventrally and becomes vertical (Fig. 6e). In *Uromastyx*, the maxillary articulation also is transformed, but the homologous surface of the ectopterygoid, still indicated by the ventral surface of the anterolateral process, is rotated such that the surface faces ventrolaterally (i.e., it is rotated in the opposite direction as in *Leiolepis*; Fig. 6f). In *Tinosaurus* sp. MPH, the maxillary facet also curves ventrally, although not as strongly as in *Leiolepis*. This feature is taken to be an apomorphic similarity between the latter two taxa.

Frontal. A frontal morphotype comprising three specimens is referred to this species on the basis of

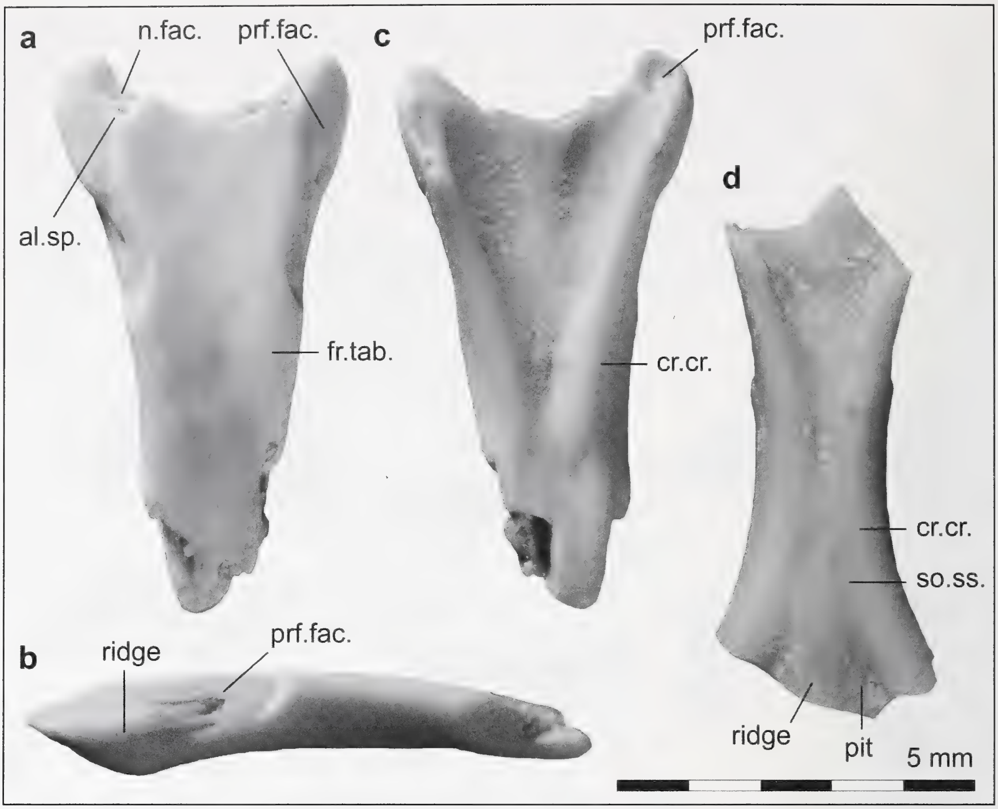

FIG. 7. Frontals of *Tinosaurus* sp. MPH. (a, b, c) PTRM 19113 in dorsal, left lateral, and ventral views, respectively; (d) PTRM 19112 in ventral view. Abbreviations: al.sp., anterolateral spine of frontal table; cr.cr., crista cranii; fr.tab., frontal table; n.fac., nasal facet; prf.fac., prefrontal facet; so.ss., groove marking insertion of solium supraseptale.

size and the presence of apomorphies uniting it with part of Agamidae*.

Description: The bone is distinctly hourglass-shaped, narrowing markedly (by 50%) from its anterior end to the mid-orbital portion (Fig. 7a). The dorsal surface of the frontal is saddle-shaped, weakly (PTRM 19113, 19467) to strongly (PTRM 19112) concave in transverse cross-section (Fig. 7a) and moderately convex in sagittal cross-section (Fig. 7b). The orbital ridges thus become especially pronounced posteriorly. The dorsal surface is nearly smooth, showing only weak irregularities in certain places (Fig. 7a), particularly on the posterior, expanding portion of the bone. The anterior portion of the bone is most completely preserved in PTRM 19113. Here, the anterior end does not show clear breaks, although broken edges (on the right side, for instance) could have been rounded by streamwear. The posterior corner of the nasal facet (n.fac.) is present at the anterolateral-most corner of the frontal table (fr.ta.). The anterolateral spine (al.sp.) of the frontal table (fr. ta.) is thin; it appears that it may also have been short, for it decays rapidly in height, although it is not clear how much its anterior extent would have been exposed dorsally, nor how much may have been removed by streamwear. Medial to the nasal facet is the lateral portion of the mediolaterally broad median spine of the frontal table; the curvature of this portion suggests the spine may have been short, but this is uncertain. As preserved, PTRM 19113 suggests that shelves for overlap of the nasals were greatly reduced, especially toward the mid-line. The prefrontal facets are U-shaped structures (Fig. 7a, b, prf.fac.).

The anterior half is divided by a longitudinal ridge into two surfaces, one facing dorsolaterally, the other ventrolaterally (Fig. 7b). The ridge extends for half the length of the facet, diminishing in prominence from anterior to posterior. Beyond the ridge, the prefrontal facet is directed entirely dorsolaterally (Fig. 7a). Tiny, shallow, well-demarcated, longitudinal grooves are found at the posterior end of the ridge (Fig. 7b).

A strong, triangular excavation for the olfactory tracts is present on the ventral surface of the frontal (Fig. 7c). There is a median swelling of the ventral surface at the anterior-most end of this excavation. The cristae cranii (cr.cr.) are low and rounded in transverse cross-section. Anteriorly, they sweep medially, closely approaching one another but never touching (Fig. 7d). Their lateral surfaces, which form also the lateral surfaces of the bone as a whole, are steep, 10–20° from the vertical. In PTRM 19467 alone there is a pair of tiny foramina on the lateral surface of each crista at mid-orbit. Medial to each crista on the posterior half of the bone is a groove, which corresponds to the attachment site for the dorsal edge of the solium supraseptale (so.ss.; cf. de Beer 1937 and Oelrich 1956). This groove deepens posteriorly, and on the right side of PTRM 19112 it

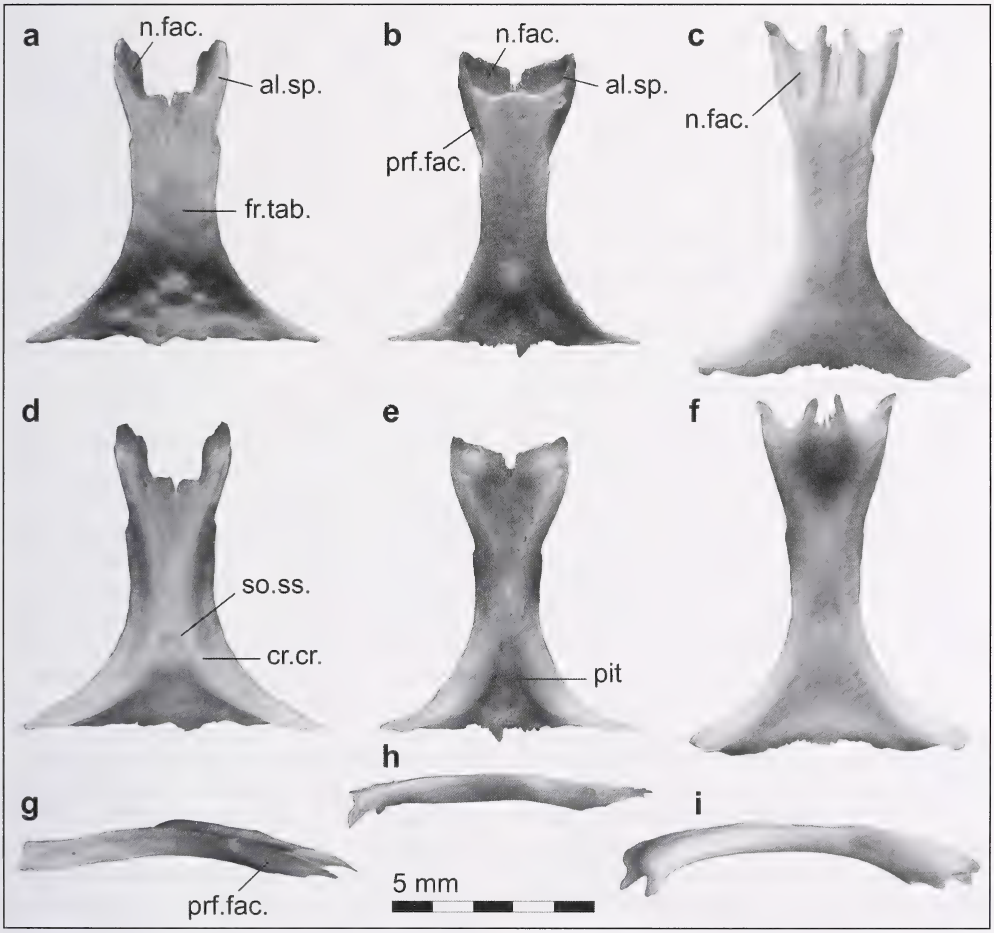

FIG. 8. Frontals of select agamids in dorsal (upper row), ventral (middle row), and right lateral (bottom row) views. (a, d, g) *Agama mossambica*, UF 55339; (b, e, h) *Leiolepis belliana*, UF 62048; and (c, f, i) *Uromastyx princeps*, CM 145044. Abbreviations: cr.cr., crista cranii; fr.tab., frontal table; n.fac., nasal facet; prf.fac., prefrontal facet; so.ss:, groove marking insertion of solium supraseptale.

appears to reach its nadir in a small pit, shallowing more posteriorly. A broad, median ridge is developed between the grooves; this ridge narrows anteriorly and attains a depth that nearly equals (PTRM 19112; Fig. 7d) and even exceeds (PTRM 19467) the depth of the cristae cranii. Anteriorly, the grooves terminate at mid-orbit in tiny impressions (Fig. 7c, d). The median ridge then has the appearance of diverging to join the cristae cranii.

Comparisons: The frontal table is concave in transverse cross-section in many acrodontans, including members of Chamaeleonidae, Agaminae (Fig. 8a), Draconinae, some Amphibolurinae (e.g., *Moloch horridus*: Bell *et al.* 2009), and *Hydrosaurus* (Smith 2009a; pers. obs.). It is also concave in many *Leiolepis* (Fig. 8b), particularly larger specimens (e.g., UF 62048, SMF 57471; cf. Smith 2009a). Although the frontal table is flat in *Uromastyx* (Fig. 8c), additional outgroup comparison (Smith 2009b) suggests that a transversely concave frontal could be primitive for Acrodonta; thus, its occurrence in *Tinosaurus* sp. MPH would be plesiomorphic.

Supraorbital flanges (Smith 2009a, b) are lacking in *Leiolepis* (Fig. 8e) and *Uromastyx* (Fig. 8f) but occur in Chamaeleonidae and many other agamid clades, such as Agaminae (Fig. 8d), some Amphibolurinae, *Hydrosaurus*, and Draconinae. This is a derived character in Iguanidae where it occurs (Smith 2009b), but its wide distribution in Acrodonta makes interpretation of this feature difficult. The absence of flanges in *Tinosaurus* sp. MPH could be primitive or derived.

In most agamids, the prefrontal facet of the frontal faces ventrolaterally in its posterior extent, and it is scarcely visible in dorsal view, even anteriorly (Fig. 8a; see also Bell *et al.* 2009, Fig. 15). In *Uromastyx*, the prefrontal facet is directed mostly laterally; *U. princeps* showed the most extensive dorsal exposure (Fig. 8c) of all examined species of the genus. Similarly, in examined chameleons, as well as all iguanids except certain members of Tropidurini and Iguaninae, the only portion of the incision exposed dorsally is that found dorsal to the longitudinal ridge on the anterior half of the scar. In *Leiolepis*, in contrast, essentially the entire posterior extent of the prefrontal facet is seen in dorsally (Fig. 8b). In this respect *Tinosaurus* sp. MPH is almost uniquely similar to *Leiolepis*.

The steep orientation of the lateral surface of the cristae cranii in *Tinosaurus* sp. MPH is uniquely similar to what is seen in *Uromastyx*, where they are also nearly vertical (Fig. 8f). In *Leiolepis*, their orientation varies slightly (cf. UF 62046 and UF 62048, Fig. 8e) but generally likens that in many other agamids (Fig. 8d).

The pit developed near the posterior end of the groove for the solium supraseptale in *Tinosaurus* sp. MPH also is well-developed in *Leiolepis* (Fig. 8e), in which it appears to relate to a particularly large projection of the posterodorsal margin of the planum. Except in *Leiolepis* it is very uncommon in examined extant agamids (cf. Fig. 8d, f), found otherwise only in *Calotes versicolor* (but not *C. mystaceus*). Such a pit also occurs in some chameleons (e.g., *Chamaeleo hoehnelii, C. laevigatus, C. roperi*), but apparently not the basal (Rieppel & Crumly 1997; Townsend & Larson 2002) *Brookesia superciliaris* (Siebenrock 1893: Fig. 40). This feature is reasonably interpreted as an apomorphy of *Leiolepis* at present, pending more extensive taxon sampling. It is shared by *Tinosaurus* sp. MPH.

The apparent mediolateral thinness of the anterolateral corners of the frontal table of *Tinosaurus* sp. MPH is similar to what is seen in *Leiolepis* and *Uromastyx* (Fig. 8b, c), but those structures are quite variable in agamids, so the significance of this observation is uncertain.

DISCUSSION

Acrodontan phylogeny is currently in flux (e.g., Amer & Kumazawa 2005a, b; Honda *et al.* 2000; Hugall & Lee 2004; Hugall *et al.* 2008; Macey *et al.* 1997, 1998, 2000; Schulte & Cartwright 2009; Schulte *et al.* 2003), and conclusions drawn from new characters discussed here must be consistent with several plausible topologies if they are to be robust to future developments. I consider here the following four hypotheses: (h1) Agamidae* is monophyletic, and *Uromastyx* and *Leiolepis* form a clade that is the sister-taxon to the rest of Agamidae* (Fig. 9a), based on Moody (1980) (see also maximum parsimony results of Honda *et al.* 2000); (h2) Agamidae* is monophyletic, and *Uromastyx* and *Leiolepis* form successively closer outgroups to the rest of the clade (Fig. 9b), based on Macey *et al.* (2000); (h3) *Uromastyx* is basal in Acrodonta, with Chamaeleonidae and *Leiolepis* as successively closer sister-taxa to the rest of Agamidae* (Fig. 9c), based on Schulte and Cartwright (2009); and (h4) *Uromastyx* and *Leiolepis* are sister-taxa, forming a clade that is basal in Acrodonta.

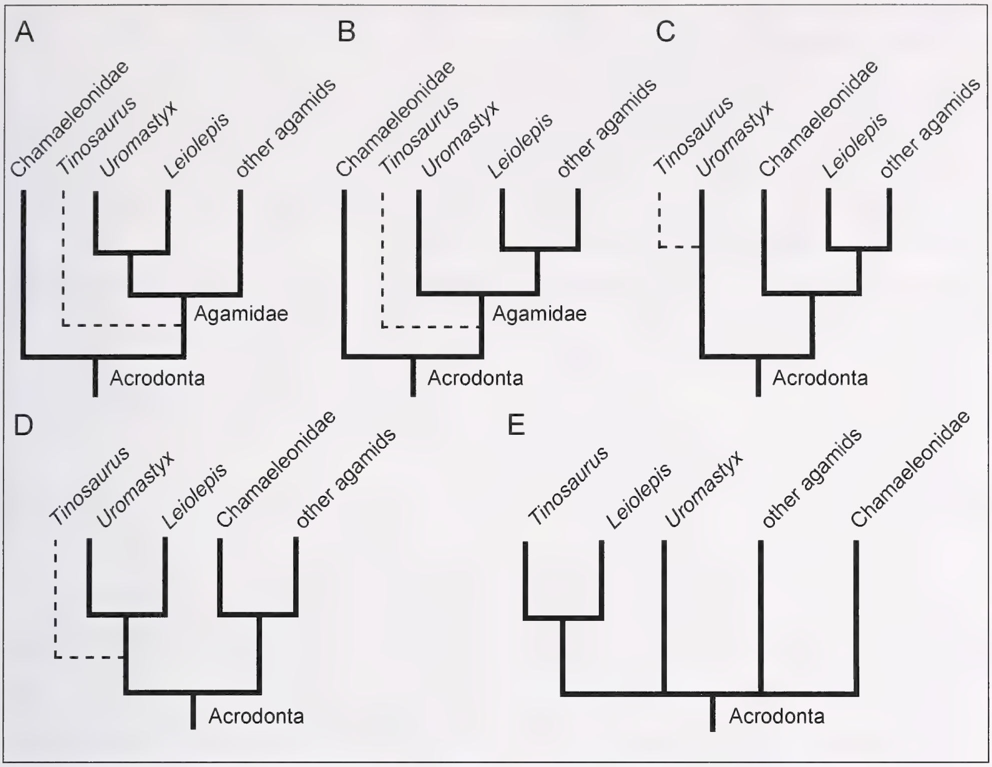

FIG. 9. Various hypotheses of the relationships of *Tinosaurus* sp. MPH within Acrodonta based on data in Table 1. Outgroup constructed using polarity decisions. In parts A–D, the described phylogenetic scaffold was enforced; part E shows unconstrained results. A. *Uromastyx* and *Leiolepis* form a clade that is the sister to the remainder of a monophyletic Agamidae (after Moody 1980; also Honda *et al.* 2000 under maximum parsimony). B. *Leiolepis* and *Uromastyx* form successive outgroups to the remainder of a monophyletic Agamidae (after Macey *et al.* 2000). C. *Uromastyx* is basal in Acrodonta, followed by Chamaeleonidae, *Leiolepis*, and the rest of Agamidae (Schulte & Cartwright 2009); D. *Uromastyx* and *Leiolepis* are sister-taxa, forming a clade that is the sister-group of other acrodontans. These topologies are not intended to cover all possibilities, nor is it implied that they are equally well supported or that the authors espouse their credited hypotheses to the exclusion of others. E. Strict consensus of 3 most-parsimonious trees (length = 13) that result from analysis of data in Table 1.

The characters noted above support a general relationship between North American *Tinosaurus* and the living clades *Uromastyx* and/or *Leiolepis*, but are partly contradictory in detail. *Tinosaurus* sp. MPH shows derived similarity to *Leiolepis* and *Uromastyx* within Acrodonta in the following two respects: strong median cleft on palatal shelf of premaxilla present; and prefrontal facet on frontal rotated to face laterally or dorsolaterally. *Tinosaurus* sp. MPH shows derived similarity to *Uromastyx* within Acrodonta in the following two respects: anterior premaxillary foramina present (at least variably); and nearly vertical orientation of lateral surface of crista cranii on frontal. *Tinosaurus* sp. MPH shows derived similarity to *Leiolepis* within Acrodonta in as many as six respects: relatively high premaxillary tooth count and well-developed lateral processes of premaxilla (depends on tree topology); palatine facet does not extend to posterior end of palatine process of maxilla; dual pterygoid articulations on ectopterygoid, separated by strong, sharp transverse ridge (relationship to condition in *Uromastyx* uncertain); high obliquity

TABLE 1. Character-taxon matrix for examining relationships of *Tinosaurus* sp. MPH. (1) Median cleft on palatal shelf of maxilla absent, 0, or present, 1. (2) Anterior premaxillary foramina absent, 0, or present, 1. (3) Premaxillary tooth count >3, 0, or ≤3, 1. (4) Palatine articulation on maxilla reaches base of palatine process on its posterior border, 0, or does not, 1. (5) Maxillary reentrant on jugal absent, 0, or present, 1. (6) Pterygoid articulates only posteriorly on ectopterygoid, 0, or possess an accessory anterior articulation, 1. (7) Maxillary facet on ectopterygoid trending dosolaterally to roughly horizontal, 0, or trending ventrolaterally, 1. (8) Lateral surface of cristae cranii on frontal strongly oblique, 0, or nearly vertical, 1. (9) Prefrontal facet on frontal hidden beneath frontal table, 0, or visible in dorsal view, 1. (10) Distinct pit for posterior attachment of solium supraseptale on frontal absent, 0, or present, 1.

	1	2	3	4	5	6	7	8	9	10
Ancestor	0	0	0	?	?	0	0	0	0	0
Uromastyx	1	1	0/1	0	1	0	0	1	1	0
Leiolepis	1	0	0	1	0	1	1	0	1	1
Tinosaurus sp. MPH	1	0/1	0	1	0	1	1	1	1	1
Chamaeleonidae	?	?	1	1	0	0	?	0	0	?
Other agamids	0	0	1	0	1	0	0	0	0	0

of maxillary facet of ectopterygoid; posterior portion of prefrontal facet completely exposed in dorsal view of frontal; and pit developed on frontal near posterior end of grooves for insertion of the solium supraseptale.

To test the relationships of *Tinosaurus* sp. MPH, I generated a topological scaffold (constraint) in PAUP* v. 4b10 (Swofford 2002) for each phylogenetic hypothesis mentioned above. Then, with the matrix in Table 1 (based on descriptions and results above), I conducted exhaustive searches for the most parsimonious position of *Tinosaurus* sp. MPH within that scaffold (as done by Bhullar & Smith 2008). The resulting position of *Tinosaurus* sp. MPH with respect to the major acrodontan clades is shown with a dashed line in Fig. 9a–d; in none of them is *Tinosaurus* sp. MPH the sister-taxon of *Leiolepis*. On the other hand, when no phylogenetic scaffold is enforced, *Tinosaurus* sp. MPH is always the sister-taxon of *Leiolepis*, regardless of where this clade falls (Fig. 9e). At the least, these results do not provide consistent support for any particular position of *Tinosaurus* sp. MPH. Nevertheless, I find the dual articulation of the pterygoid on the ectopterygoid particularly compelling, and the ectopterygoid is perhaps the most securely referred element. Thus, in the brief discussion below I will treat *Tinosaurus* sp. MPH as if it were securely related to *Leiolepis*.

The earliest record of North American *Tinosaurus* is from the early Eocene (middle Wasatchian, approximately zone Wa4) of Wyoming (Smith 2006b). Assuming that Acrodonta invaded North America only one time, then these remains must also be attributed to the stem of *Leiolepis*, and one may thus conclude that *Leiolepis* had diverged from other acrodontans by the early Eocene. Stem representatives of *Uromastyx*, which under each of the phylogenetic hypotheses summarized in Figure 9a–d should have diverged from other agamids at the same time as or prior to *Leiolepis*, are well represented in the Paleogene of Asia beginning in the early Eocene (Alifanov 2009; Averianov & Danilov 1996).

Direct dispersal of stem-*Leiolepis* from Asia to North America in the early Eocene (cf. Moody 1980) would be one possible interpretation of these data. Yet, the phylogenetic position of European species of *Tinosaurus* from the early Eocene (Augé 1990, 2005; Augé & Smith 1997; Augé *et al.* 1997; Hecht & Hoffstetter 1962; Rage & Augé 2003) must be constrained before a route passing first across the Turgai Strait into Europe and thence North America could comfortably be excluded. To be sure, extant *Leiolepis* are ground-dwellers that prefer open formations (Losos *et al.* 1989) and dig deep burrows (Pianka & Vitt 2003), which may decrease the probability of dispersal by rafting over large water bodies. On the other hand, they are common inhabitants of beach environments (e.g., Losos *et al.* 1989), and the earliest occurrence of *Tinosaurus* in Europe (earliest Eocene: Augé 2005, Augé & Smith 1997) appears to precede its earliest occurrence in North America (Smith 2006a). Still, *Tinosaurus* is rare in the early

Eocene of North America (Smith 2006a), and thus its (true) first historic appearance is not well constrained.

The Eocene record of fossil lizards of North America clearly shows that many taxa presently found in the tropics once had extratropical distributions (Gauthier 1982; Smith 2006a, 2009a, 2011), which presumably relates to the warm, wet, and equable climates of the Eocene. North American *Tinosaurus* suggests the possibility that the agamid lizard *Leiolepis* could show a similar pattern. However, determining whether the historical distribution of this or other tropical agamids also conform to this pattern will require a much more intensive sampling of and attention to the fossil record of the group.

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APPENDIX

Modern comparative osteological specimens examined for this study: Agaminae: *Acanthocercus cyanogaster* (UF 50556), *Agama mossambica* (UF 55339, 55352), *Laudakia stellio* (CM 39115, 39116, UF 68087), *Phrynocephalus maculatus* (UF 71573, 71574), *P. interscapularis* (UF 80248), *Pseudotrapelus sinaitus* (UF 13934), *Trapelus agilis* (UF 74674, 74675), *T. megalonyx* (UF 67819), *T. pallidus* (CM 41289), *T. ruderatus* (UF 71720, 71721); Amphibolurinae: *Physignathus cocincinus* (SMF 61415, UF 71685, 71686), *Pogona vitticeps* (SMF 71829); Draconinae: *Acanthosaura armata* (UF 69015), *Bronchocela cristatella* (UF 42346, 51820), *Calotes mystaceus* (SMF 69754), *C. versicolor* (UF 68490, 71577), *Draco volans* (UF 53599), *Gonocephalus grandis* (UF 61544, 61548), *Japalura polygonata* (UF 63381, 63382), *Lyriocephalus scutatus* (UF 68088), Hydrosaurinae: *Hydrosaurus amboinensis* (SMF 70930); Leiolepidinae: *Leiolepis belliana* (SMF 57471, UF 62046–62048); Uromastycinae: *Uromastyx acanthinurus* (UF 54136), *U. geyri* (UF 144229), *U. hardwickii* (CM 145030, 145031, 145037), *U. princeps* (CM 145043, 145044); Chamaeleonidae: *Chamaeleo chamaeleon* (SMF 33202), *C. hoehnelii* (CM 144863, 144865), *C. roperi* (SMF 84618).